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Factors affecting trembling aspen (*Populus tremuloides* Michx.) health in the boreal forest of Alberta, Saskatchewan, and Manitoba, Canada

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Abstract

The value of trembling aspen (*Populus tremuloides* Michx.) as a resource has increased in Canada in recent years, but key information regarding the health of this species and its interrelationships with biotic and abiotic agents is lacking. A regional study was conducted to (i) assess the general health of trembling aspen trees in the three prairie provinces of Canada, (ii) determine the incidence of biotic and abiotic agents affecting these trees and (iii) determine what factors most influenced the health of trembling aspen trees between forest tent caterpillar (*Malacosoma disstria* Hübner) outbreaks. A total of 8296 trembling aspen trees in 85 plots were monitored during 1992–1994. Trembling aspen health was assessed and related to biotic and abiotic damage agents and symptoms. Trembling aspen in the study area were generally healthy: crowns were in good condition, trees had few pests, and mortality rates were low. Confidence intervals for proportion of trees dead less than 2 years are reported by age class. Large aspen tortrix (*Choristoneura conflictana* [Wlk.]) and poplar peniophora (*Peniophora polygonia* [Pers.:Fr.]) Boud. were the most common pests, occurring on 15 and 13% of live trees, respectively; incidences of other pests were <7%. Significant associations between incidences of pests and several stand characteristics were found. Regression analysis showed tree age, a climate moisture index, number of years of forest tent caterpillar defoliation, and incidence of *Armillaria* root disease (*Armillaria* spp.) accounted for a significant proportion of the variation in trembling aspen health and mortality. Our results highlight the need to consider pests, especially forest tent caterpillar and *Armillaria* root disease, in the management of trembling aspen or in landscape-level simulations of trembling aspen productivity.
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Keywords: *Populus tremuloides*; Forest health; Pests; Drought

1. Introduction

Trembling aspen (*Populus tremuloides* Michx.) is one of the most common tree species in the boreal forest of Alberta, Saskatchewan, and Manitoba, Canada. This tree species is also the most important tree species in the aspen parkland, a transitional zone between the boreal forest to the north and the grassland

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of the prairies to the south. Trembling aspen accounts for 37% of the gross merchantable volume in the productive forests of the three prairie provinces (Canadian Council of Forest Ministers, 1997). This species has also become increasingly important to the forest products industry in the region in the past 20 years. Roundwood hardwood production, of which trembling aspen is the principal species harvested, has increased from 794 000 m^3 in 1970 to 8 045 000 m^3 in 1995 (Canadian Council of Forest Ministers, 1997).

Trembling aspen in the aspen parkland have deteriorated in general condition because of drought, repeated defoliation by forest tent caterpillar (*Malacosoma disstria* Hübner), or both (Zoltai et al., 1991; Hogg and Schwarz, 1999). Concerned citizens have speculated that agricultural activity, forest fragmentation, exclusion of forest fire following settlement, late spring frosts, and air pollution may also play a role in the observed deterioration. These factors may not have affected trembling aspen in the more northern boreal forests where large tracts of land have not been cleared for agricultural purposes. While fires now occur less frequently in the boreal forest because of improvements in fire suppression programs, fires in the transitional forest have been more or less excluded by the same suppression programs (Van Wagner, 1978; Barney and Stocks, 1983; Weir, 1996). Emissions of sulfur and nitrogen compounds are relatively low regionally (<2 kg ha per year) (Cheng, 1994; McDonald et al., 1993) compared to eastern North America and Europe, but may be important locally near point sources. The level of oil exploration, particularly in the western portion of the study area, is high and much land has been cleared for seismic lines, oil and gas wells, and pipelines (Bella, 1986).

As the value of the trembling aspen resource has increased, forest managers have become aware of a lack of key information regarding the interrelationships between trembling aspen and insects and diseases (Peterson and Peterson, 1992). Basic information on the biology of major trembling aspen pests such as forest tent caterpillar, large aspen tortrix (*Choristoneura conflictana* [Wlk.]) *Armillaria* root disease (*Armillaria* spp.), false tinder conk (*Phellinus tremulae* [Bond.] Bond. and Boriss.), and poplar peniophora (*Peniophora polygonia* [Pers.:Fr.] Boud.) is available (e.g., Ives and Wong, 1988; Hiratsuka, 1987), but there is a dearth of information on the impacts of these and other pests and how they operate in trembling aspen stands of different ages and stand densities across landscapes or in a regional context.

Forest tent caterpillar is the most consequential pest of trembling aspen in the prairie provinces, the last major outbreak ending in 1990 (Brandt, 1995a). Outbreaks of this insect lead to reductions in growth and tree mortality (Barter and Cameron, 1955; Hildahl and Reeks, 1960). Thus, forest tent caterpillar is conjectured to be a major driver of aspen stand dynamics. Mattson and Addy (1975) first raised the hypothesis that defoliators regulate primary production of boreal forest stands. They used the forest tent caterpillar/trembling aspen interaction as an example to support this conjecture. Others have provided some evidence of an interaction between forest tent caterpillar and opportunistic secondary organisms (Churchill et al., 1964). While this information is essential to understand factors affecting productivity and health of trembling aspen stands, it does not increase our understanding about what happens in trembling aspen stands between outbreaks of forest tent caterpillar in terms of tree condition, mortality, and other pests.

This study was undertaken to (i) assess the general health of trembling aspen trees in the boreal forests of Alberta, Saskatchewan, and Manitoba, (ii) determine the incidence of biotic and abiotic agents that damage trembling aspen trees in these forests and (iii) determine what factors most influenced the health of trembling aspen trees between forest tent caterpillar outbreaks.

2. Methods

2.1. Study area, plot selection and assessment

The study area included three Canadian provinces: Alberta, Saskatchewan, and Manitoba. Eighty-five plots were selected at random from lists of trembling aspen permanent sample plots obtained from forest management agencies in the prairie provinces. Plots were square or rectangular in shape and ranged in size from 500 to 2023 m^2. To the extent that the plots were representative of conditions across the study area, the results should reflect the health status of trembling aspen trees in the region. Permanent sample plots were

examined to take advantage of growth and yield data collected at these sites by provincial forest management agencies. Each plot was visited once during either June, July, or August of 1992, 1993, or 1994.

Each tree in the permanent sample plots was assessed by examining the tree's condition and the incidence of insects, diseases, and abiotic damage symptoms. Tree condition was categorized as healthy, weakened, declining, dead less than 2 years (dead trees with small twigs and bark still attached), or dead more than 2 years. Healthy trees were those with full, green crowns with no apparent major defects. Weakened trees were those with less than a full crown or with some evidence of insect or disease attack. Declining trees were trees with poor crowns of low vigor or with severe insect or disease damage. Pest occurrence and damage by abiotic agents were assessed on the butt, stem, crown, and foliage by recording the symptoms and signs, identifying the causal agent, and estimating the extent and severity of the damage on each tree in each plot. In the case of recently dead trees, the root collar and nearby roots were examined as well and the most probable cause of death was identified.

2.2. Ancillary data and data summarization

Data collected during field sampling were merged with growth and yield data from provincial records as well as from several other data sets in preparation for analyses. Plot tree data included diameter at breast height for each plot tree, height of each tree for plots located in Saskatchewan and Manitoba, and height of about 10–60% of the trees from plots located in Alberta. Age was estimated by using a hand lens to count growth rings on increment cores from 2 to 4 overstory trees within the plots or inferred from forest inventory maps. Records of past forest tent caterpillar defoliation were obtained from published reports (see Moody and Amirault (1992) for a listing of reports for the period 1937–1988 and Brandt (1995a) for the period 1988–1992) and archived maps of the Canadian Forest Service's Forest Insect and Disease Survey. This information was used to determine the number of years of defoliation since 1937 at each study site. Climate data obtained from Atmospheric Environment Service of Environment Canada were used to calculate a climate moisture index (cm per year) for each site based on the Jensen–Haise approach described by Hogg (1997). Values less than 0 are indicative of conditions where precipitation is less than potential evapotranspiration; values greater than 0 are indicative of conditions where precipitation exceeds potential evapotranspiration.

2.3. Statistical analyses

Two methods were used to assess the influence of various factors on trembling aspen tree condition. The first method involved two-way contingency tables in SAS (FREQ procedure, SAS Institute, 1999) where data for individual trees were utilized to assess the role of single factors. Trees dead for more than 2 years were not used in these analyses because of the uncertainty of when they died. As the scale of measurement of both the response and explanatory variables were ordinal, the Mantel–Haenszel chi-square statistic was used to test the null hypothesis of lack of linear association with the significance level set at $\alpha = 0.05$. In each univariate analysis, tree condition was the polytomous response variable. Tree age, tree height, diameter at breast height, the number of years of forest tent caterpillar defoliation, the climate moisture index, and the presence or absence of *Armillaria* root disease were the polytomous explanatory variables. The scale of measurement and levels of all response and explanatory variables for these tests are listed in Table 1. Adjusted residuals (Agresti, 1996) were calculated using the GENMOD procedure (SAS Institute, 1999) and were used to assess lack of fit of the null hypothesis on a cell by cell basis in contingency tables. A 95% confidence interval for proportions (Steel et al., 1997) was calculated by age class for recently dead trees.

The second method involved step-wise regression to model the combined effects of various factors on tree condition (REG procedure, SAS Institute, 1999). Two models were developed. In the first, the dependent variable was the percent of plot trees that were healthy. In the second, the dependent variable was the percent of plot trees that were dead but standing. The independent variables tested for both models included plot values for the number of years of forest tent caterpillar defoliation, tree age, the climate moisture index, and incidence of *Armillaria* root disease expressed as a percentage. The significance level

Table 1
Scale of measurement and levels of variables used in tests of association between the response variable, tree condition, and various explanatory variables

Variable	Scale of measurement	Levels
Tree condition	Ordinal	Healthy Weakened Declining Dead
Age	Ordinal	<40 years 40–80 years >80 years
Height	Ordinal	<10 m 10–20 m >20 m
Diameter at breast height	Ordinal	<10 cm 10–20 cm >20 cm
No. of years of forest tent caterpillar defoliation	Ordinal	Sites experiencing 1 year of defoliation Sites experiencing 2–3 years of defoliation Sites experiencing ≥4 years of defoliation
Armillaria root rot	Ordinal	Present Absent
Climate moisture index	Ordinal	<5, dry 5–15, intermediate >15, moist

for adding or keeping a variable in the model was $\alpha = 0.15$ and 0.10, respectively. Additionally, a test for heteroscedasticity (White, 1980) was conducted, collinearity diagnostics and influence statistics (Belsley et al., 1980; Freund and Littell, 1991) were calculated, and various diagnostic plots were produced for both models using the REG procedure in SAS.

The presence or absence of various pests in relation to tree and stand characteristics were also tested using two-way contingency tables. The Mantel–Haenszel chi-square statistic was used to test the null hypothesis of lack of linear association with a significance level of $\alpha = 0.05$. The scale of measurement and levels of all response and explanatory variables for these tests are listed in Table 2. Adjusted residuals were used to assess lack of fit of the null hypothesis in cells of the contingency tables. A 95% confidence interval for proportions was calculated for the various pests or types of damage detected during the assessments.

Table 2
Scale of measurement and levels of variables used in tests of association between the presence or absence of various pests (the response variable) and various explanatory variables

Variable	Scale of measurement	Levels
Pest	Ordinal	Present Absent
Density	Ordinal	<1000 stems/ha 1000–2000 stems/ha >2000 stems/ha
Age	Ordinal	<40 years 40–80 years >80 years
Height	Ordinal	<10 m 10–20 m >20 m
Diameter at breast height	Ordinal	<10 cm 10–20 cm >20 cm

Fig. 1. Locations of study sites in Alberta, Saskatchewan, and Manitoba, Canada, where factors affecting the condition of trembling aspen were assessed between 1992 and 1994.

3. Results

The 85 plots sampled were distributed across the study area (Fig. 1). Mean diameter at breast height and height of trees within plots was 16.1 cm and 16.4 m, respectively (Table 3). The mean age of trees was 64.5 years. Stands where plots were located were generally well stocked, but density of trembling aspen stems ranged from a high of 14 140 stems/ha to a low of 40 stems/ha. On average, trembling aspen trees accounted for 69% or more of the stems sampled at each site.

Of the 8296 trembling aspen trees assessed during the study 60.4% were healthy. Weakened trees accounted for 13.6%, declining trees for 3.2%, and the remainder 22.8% were dead. Although the percentage

Table 3
Attributes of 85 trembling aspen study sites assessed in Alberta, Saskatchewan, and Manitoba, Canada, between 1992 and 1994

Attribute	Mean	Standard deviation	Range
Diameter at 1.3 m (cm)	16.1	7.3	4.8–34.6
Tree height (m)	16.4	5.2	5.7–27.6
Age (years)	64.5	29.3	16–149
Stems/ha	1896	2047	40–14 140
Aspen cover (%)	69.0	26.1	5–100
Elevation (m)	548	245	230–1510
Percentage of healthy trees	58.4	24.6	0–100
Percentage of weakened trees	16.4	16.0	0–76.9
Percentage of declining trees	3.8	6.4	0–33.3
Percentage of trees dead <2 years	6.8	8.3	0–33.3
Percentage of trees dead ≥2 years	14.6	16.8	0–70.8

Table 4
Proportion of dead trees (<2 years since mortality) and the 95% confidence intervals for the proportions based on age class

Age class (years)	Number of trees sampled	Proportion dead	95% confidence interval[a]	
			Low	High
<40	2011	0.195	0.178	0.212
40–80	4145	0.073	0.065	0.081
>80	996	0.055	0.041	0.069

[a] CI calculated per Steel et al. (1997).

of dead trees was high, this represents the cumulative mortality at the study plots over several years. Mean percentages of healthy, weakened, declining, and dead aspen trees by plot were slightly different than above and were 58.4, 16.4, 3.8, and 21.4%, respectively.

A summary of mortality by age class indicates that most of the recent mortality (i.e., less than 2 years) occurred in the youngest age class (Table 4). A 2-year mortality rate of 19.5% occurred in trees less than 40 years old, while in the other two age classes, rates were 7.3 and 5.5%. The 95% confidence intervals for the proportion of dead trees in the older two classes overlap, while the confidence intervals for the youngest and intermediate age classes do not. This suggests that the mortality rate for the youngest class is significantly higher than that of the two older classes, while the mortality rates of the older classes do not differ.

In each age class, height class, and diameter class, healthy trees accounted for the highest proportion of the living trees followed by weakened and then declining trees (Fig. 2). As would be expected, there was a significant association between tree condition and tree age, tree height, and diameter at breast height ($P = 0.001$).

Signs and symptoms of major pests or defects were absent from 59% of trees assessed (Table 5). Most of the remaining 41% of trees, however, were not severely at risk of death. Only two pests, large aspen tortrix and poplar peniophora, occurred at frequencies of 10% or more, while a few other pests including an unidentified defoliator (probably *Chrysomela* spp.), leafblotch miner (*Phyllonorycter salicifoliella* [Cham.]), an unidentified stem canker, and false tinder conk, occurred at frequencies near 5%. Mechanical damage from falling trees and rubbing of adjacent trees was found on 8% of the trees assessed. Crown dieback, which includes branch and twig mortality, dead tops, and broken stems, occurred on 5% of the trembling aspen trees sampled.

Historical accounts of forest tent caterpillar defoliation examined indicate several major outbreaks have occurred in the prairie provinces since 1937. Periods of extensive and severe defoliation occurred during 1937–1945, 1952–1953, 1960–1964, 1974–1977, 1978–1983, and 1986–1990. In terms of years of defoliation since 1937, 24% of the sites were defoliated 4 or more years, 31% of the sites were defoliated 2 or 3 years, while the remainder (44%) of the sites received 1 year or none.

An increasing number of years of forest tent caterpillar defoliation was associated with an increased proportion of weakened, declining, and dead trees ($P = 0.001$) at the study sites. Trees were found to be in better condition on moist sites than on intermediate or dry sites as indicated by the climate moisture index ($P = 0.001$). Finally, the presence of *Armillaria* root disease was significantly associated with tree condition ($P = 0.001$) when controlling for the number of forest tent caterpillar outbreaks. The incidences of this disease in the weakened, declining, and dead classes were higher than expected (based on adjusted residuals) in stands that experienced one or two forest tent caterpillar outbreaks than in outbreak-free stands.

The best-fitting model for percent healthy trees accounted for 41.8% of the variation based on the adjusted R^2 ($F = 16.10$, $P < 0.0001$). Significant factors ($\alpha = 0.05$) included years of forest tent caterpillar defoliation, tree age, the climate moisture index, and the percentage of trees affected by *Armillaria* root disease (Table 6). In general, the percentage of healthy trees increases as the number of years of forest tent caterpillar defoliation, tree age and the incidence of *Armillaria* root disease decreases, and the CMI increases. Ranking these factors based on their contribution to the total variation indicates that tree age was most important at 18.1% followed by the climate moisture index at 10.6%, forest tent caterpillar defoliation at 9.8% and *Armillaria* root disease at 6.1%. The errors were not heteroscedastic (d.f. = 14, $\chi^2 = 11.98$, $P = 0.6081$); consequently transformation of data were unnecessary. Errors were also normally distributed based on the results of a normal probability–probability

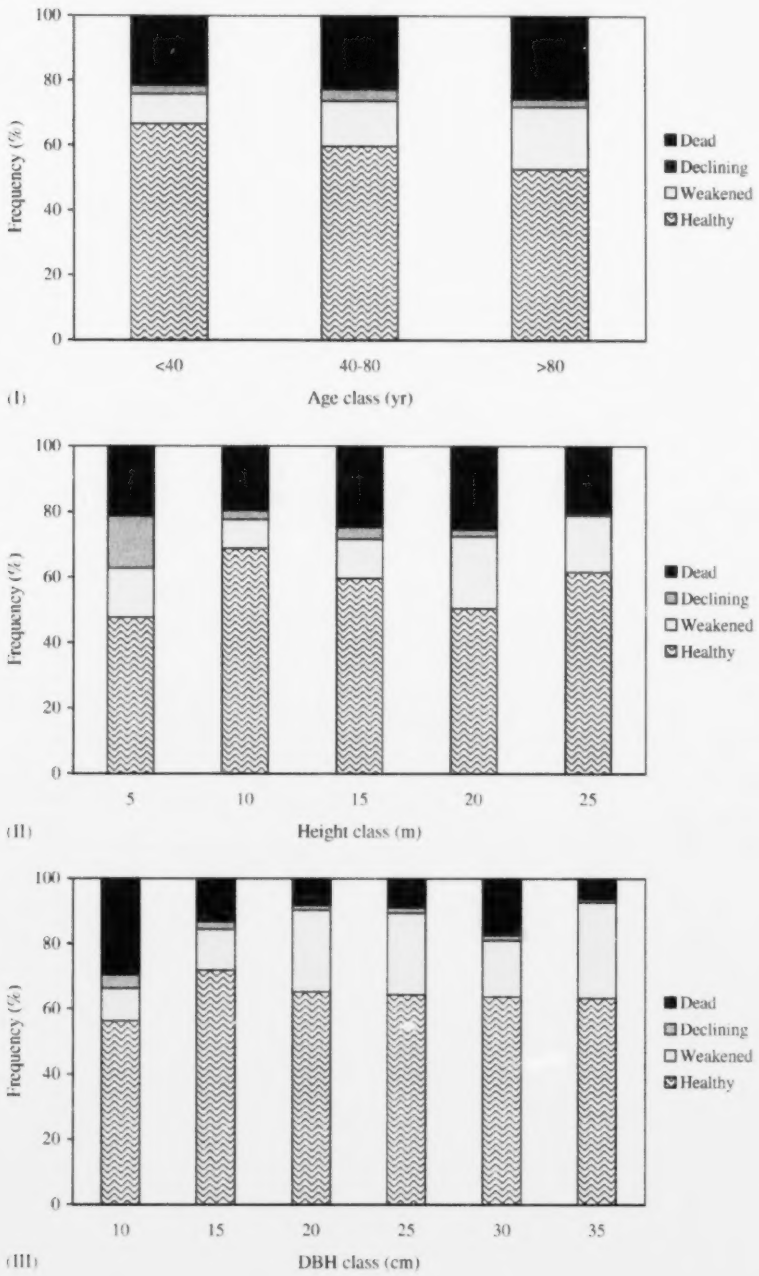

Fig. 2. Histograms of aspen tree condition by (i) tree age, (ii) tree height, and (iii) diameter at breast height (1.3 m). Healthy trees had no apparent defects. Weakened trees had less than full crowns or had evidence of moderate insect or disease attack. Declining trees had poor crowns of low vigor or had severe insect or disease symptoms.

Table 5
Pests or defects associated with trembling aspen in the prairie provinces of west-central Canada (based on assessments of living trembling aspen trees ($n = 6401$) made between 1992 and 1994)

Pest or defect	Trees affected		95% confidence interval[a]	
	Number	Proportion	Low	High
None	3774	0.590	0.578	0.602
Insects				
Large aspen tortrix, *C. conflictana*	950	0.148	0.139	0.157
Unidentified defoliator(s)	368	0.057	0.051	0.063
Leafblotch miner, *P. salicifoliella*	346	0.054	0.048	0.060
Poplar borer, *S. calcarata*	186	0.029	0.025	0.033
Aspen leaf beetle, *C. crotchi*	186	0.029	0.025	0.033
Aspen leafroller, *P. oregonana*	128	0.020	0.017	0.023
American aspen beetle, *G. americana*	49	0.008	0.006	0.010
Fungi				
Poplar peniophora, *P. polygonia*	804	0.126	0.118	0.134
Unidentified stem canker(s)	413	0.065	0.059	0.071
False tinder conk, *P. tremulae*	329	0.051	0.046	0.056
Armillaria root disease, *Armillaria* spp.				
On living trees	11	0.002	0.001	0.003
On dead trees[b]	108	0.144	0.119	0.169
Hypoxylon canker, *E. mammata*	48	0.007	0.005	0.009
Mammals				
Snowshoe hare, *Lepus americanus*	97	0.015	0.012	0.018
Defects				
Animal or mechanical damage	533	0.083	0.076	0.090
Crown dieback	350	0.055	0.049	0.061
Stem crack	282	0.044	0.041	0.047
Stem crook	264	0.041	0.036	0.046
Severe lean	158	0.025	0.021	0.029

[a] CI calculated per Steel et al. (1997).
[b] There were 751 trees that were dead less than 2 years; *Armillaria* root rot was found on 108 of these trees.

Table 6
Results of step-wise regression for two models[a]

Dependent and independent variables	Parameter estimate	Standard error	Type II sums of squares	*F*-value	Probability > *F*
Percentage of healthy trees					
Intercept	82.13401	5.59551	75743.00	215.46	<0.0001
Years of forest tent caterpillar defoliation (year)	−3.18854	0.92337	4191.82	11.92	0.0009
Tree age (year)	−0.35897	0.07432	8201.38	23.33	<0.0001
Climate moisture index (cm per year)	1.17152	0.31174	4964.59	14.12	0.0003
Incidence of *Armillaria* root disease (%)	−2.35297	0.79500	3079.44	8.76	0.0040
Percentage of standing dead trees					
Intercept	9.48790	4.30361	983.94	4.86	0.0304
Years of forest tent caterpillar defoliation (year)	1.48834	0.70125	911.91	4.50	0.0369
Tree age (year)	0.18945	0.05711	2228.06	11.01	0.0014
Climate moisture index (cm per year)	−0.75531	0.23669	2061.60	10.18	0.0020
Incidence of *Armillaria* root disease (%)	1.82780	0.60529	1845.98	9.12	0.0034

[a] The dependent variables were (i) the percent of plot trees that were healthy and (ii) the percent of plot trees that were dead but standing.

plot. There was no evidence of multicollinearity among the four independent variables in the model using the criteria of Belsley et al. (1980). Four outliers were identified but were left in the data set for the regression analysis because no obvious errors were found to be associated with the observations.

For percent standing dead trees, the best-fitting model accounted for 27.9% of the total variation based on the adjusted R^2 ($F = 9.13$, $P < 0.0001$). As with the previous model, all factors tested were significant at $\alpha = 0.05$ (Table 6). The percentage of standing dead trees increases as the number of years of forest tent caterpillar defoliation, tree age, and the incidence of *Armillaria* root disease increases, and the CMI decreases. *Armillaria* root disease (10.5%) contributed most to the total variation in percent standing dead trees followed by tree age (8.7%), the climate moisture index (8.2%), and forest tent caterpillar defoliation (4.0%). The test for heteroscedasticity was negative (d.f. = 14, $\chi^2 = 13.63$, $P = 0.4773$) and errors were normally distributed. No support for the presence of multicollinearity among model parameters was detected in the collinearity diagnostics. Influence statistics indicated the presence of three outliers. These data were examined for discrepancies but none were detected. Thus, these data were retained in the data set for the regression analysis.

Incidence of large aspen tortrix was associated with stem density, diameter at breast height, height, and age ($P = 0.001$). Large, older trees were more likely to be affected by large aspen tortrix. The insect was most prevalent in stands with less than 1000 stems/ha and was never observed in stands with greater than 2000 stems/ha. In terms of tree diameter, trees most susceptible to defoliation by large aspen tortrix were those with diameters greater than 20 cm while those trees with diameters between 10 and 20 cm were only slightly less frequently defoliated; small trees were rarely defoliated. Similar results were obtained for tree height, with the largest height class being most frequently defoliated followed by the middle and then the smallest height classes. Trees between 40 and 80 years old were most frequently defoliated while trees less than 40 years old were rarely defoliated.

Of lesser importance, leafblotch miner was significantly associated with increasing stem density, and decreasing diameter, height, and age ($P = 0.001$). This insect was most abundant in young stands with small trees. The occurrence of poplar borer (*Saperda calcarata* Say) and aspen leafroller (*Pseudexentera oregonana* [Wlsm.]) was also associated with stem density, diameter at breast height, height, and age ($P = 0.001$). Poplar borer was most prevalent in low-density stands while aspen leafroller only occurred in stands with 1000–2000 stems/ha. Trees with diameters between 10 and 20 cm and heights between 10 and 20 m were more frequently infested by both poplar borer and aspen leafroller. This relationship also occurred with respect to tree age with both young (<40 years) and old (>80 years) trees rarely affected.

Decreasing incidences of *Armillaria* root disease and hypoxylon canker (*Entoleuca mammata* [Wahlenberg] J.D. Rogers and Y.M. Yu) were associated with increasing stem density ($P = 0.001$). Incidence of *Armillaria* root disease was not associated with diameter ($P = 0.164$), height ($P = 0.750$), or age ($P = 0.097$). Incidence of hypoxylon canker was also not associated with either tree diameter ($P = 0.992$) or height ($P = 0.176$) but was associated with age ($P = 0.034$), with trees between 40 and 80 years old most frequently infected.

The incidences of the stem decays, poplar peniophora and false tinder conk, were associated with stem density, diameter at breast height, height, and age ($P = 0.001$). Poplar peniophora was by far most common in stands with stem densities between 1000 and 2000 stems/ha while false tinder conk was most common in stands with less than 1000 stem/ha. Similar relationships for both decays were borne out in relation to diameter, height, and age. For example, poplar peniophora was most prevalent in the smaller and younger trees, which generally occurred in higher density stands, while false tinder conk was most prevalent in the larger and older trees, which generally occurred in the low-density stands.

Dieback was associated with stem density, height, and stand age ($P = 0.001$) but was not associated with diameter ($P = 0.065$). Dieback was most prevalent in taller, older trees in stands with stem densities of less than 2000 stems/ha.

4. Discussion

Trembling aspen in the study area are generally in healthy condition as attested to by the fact that most

trees have a healthy crown with low incidences of pests, and mortality rates of trees are relatively low. Mortality rates based on recently dead trees were higher than those reported by others, but this is the cumulative mortality for trees dead less than 2 years. In Michigan, Minnesota, and Wisconsin, trembling aspen annual mortality rates were 12.1% for trees less than 10 cm in diameter, 9.4–1.6% for trees between 10 and 20 cm in diameter, and 1.4% for trees greater than 20 cm in diameter (Buchman, 1983). Trembling aspen annual mortality rates of 6% or less were found in trembling aspen stands in Wisconsin (Jepsen et al., 1996). The high mortality rates we observed in the youngest age class is consistent with findings of others. In young trembling aspen stands, trees die during periods of natural thinning, usually the result of infestations by various pests (Peterson and Peterson, 1992). In the Lake States, trembling aspen experiences periods of accelerated thinning in stands less than 25 years old (Graham et al., 1963).

The 95% confidence intervals for the proportions of living trees infested by the more common pests encountered in this study and the incidence of these pests in relation to stand characteristics should prove useful for ecological modelers interested in landscape-level simulations. Our analyses provide evidence that many pests are associated with specific stand conditions in the study area. For example, large aspen tortrix and poplar borer appear to prefer aspen stands with larger, more widely spaced trees. *Armillaria* root disease and hypoxylon canker appear to be thinning out trees as both pests are found in the less dense stands. Poplar peniophora prefers younger, smaller, and more dense stands of trembling aspen while false tinder conk is more prevalent in older, larger, less dense stands. While some of this information is available at the stand level for the study area (e.g., Baranyay, 1967; Ives et al., 1973), our study provides new data based on surveys of trembling aspen stands distributed across the prairie provinces. The information also improves our ability to predict which pests are important in trembling aspen stands between major outbreaks of forest tent caterpillar.

Dieback of trembling aspen in the boreal forest of our study area is associated with specific stand conditions (i.e., mature, less dense stands). Severity of dieback was also low, with 5.5% of trees exhibiting these symptoms. Hogg and Schwarz (1999) reported widespread dieback in trembling aspen stands along the southern boundary of the mixedwood section of Rowe (1972) near St. Walburg, Saskatchewan. Crown dieback of more than 40% was observed on 25% of the sampled trembling aspen trees of their study. Taking the current and previous studies together, dieback of trembling aspen in west-central Canada appears to be limited mostly to the transitional forest between the grasslands and the continuous boreal forest and the drier southern sites of the boreal forest. This however requires further investigation. Besides the effect of drought, no other influence of climate was assessed in our study. Late spring frosts occur in the study area periodically and have been linked to abnormal leaf flushing and dieback (Cayford et al., 1959; Zalasky, 1976; Hiratsuka and Zalasky, 1993). Several researchers have linked regional diebacks of several trees species to thaw–freeze events (Auclair et al., 1990, 1992; Becker, 1989; Landmann, 1993; Bertrand et al., 1994; Braathe, 1995; Zhu et al., 2000). Shoot blights such as Venturia leaf and shoot blight (*Venturia macularis* [Fr.:Fr.] E. Müller and Arx) or repeated, severe insect defoliation by an insect such as forest tent caterpillar may have also played a role in the observed dieback.

Based on the statistical analyses, four factors had a significant effect on trembling aspen health and mortality: years of forest tent caterpillar defoliation, age, drought, and the incidence *Armillaria* root disease. Our regression models show that after age and drought, pests have a major influence on aspen health and mortality with forest tent caterpillar and *Armillaria* root disease accounting for 15.9 and 14.6% of the total variation in the percentage of healthy trees and standing dead trees, respectively. The contribution of these two factors to the total variation highlights the importance of these pests to the health and productivity of trembling aspen. It also highlights the need for forest managers to consider these pests in management of trembling aspen stands. The remainder of the variation not accounted for by each model is likely due to effects of biotic agents that we were unable to capture during our health assessments, edaphic factors such as nutrient availability, other climate parameters, and error.

There were no forest tent caterpillar outbreaks concurrent with our study but our results indicate forest tent caterpillar defoliation continues to be a significant factor in trembling aspen health after the collapse of outbreaks. Periodic outbreaks of forest tent

104-05979/

caterpillar typically last 3–4 years. Reduction in tree growth during outbreaks generally ranges from 50 to 75% of pre-outbreak growth levels (Barter and Cameron, 1955; Rose, 1958; Hildahl and Reeks, 1960; Ives, 1971). Crown dieback is another symptom of forest tent caterpillar defoliation (Batzer et al., 1954; Gross, 1991). The impact of forest tent caterpillar on tree mortality is more controversial. Several studies in Canada and the United States have found no differences in mortality in aspen stands that were defoliated to various degrees (Ghent, 1958; Duncan and Hodson, 1958; Hildahl and Reeks, 1960). In Minnesota, however, Churchill et al. (1964) re-examined the same aspen plots established by Duncan and Hodson (1958) and found increasing mortality with increasing levels of defoliation several years following the collapse of the outbreak. More recently, studies in Alberta and Saskatchewan have demonstrated that forest tent caterpillar defoliation significantly affects growth of trembling aspen and is strongly associated with crown dieback, which is evident several years following the outbreak (Hogg and Schwarz, 1999; Hogg et al., 2002). Our results considered together with those of the previous studies suggest that forest tent caterpillar has an important effect on the regulation of aspen stand productivity and is a factor in both crown dieback and tree mortality several years following the collapse of an outbreak.

Our results support the hypothesis that *Armillaria* root disease is a primary pathogen affecting the health of trembling aspen in the study area. The incidence of this disease was associated with aspen health even when controlling for the effect of forest tent caterpillar defoliation on tree condition. Primary disease can be viewed as a continuum, beginning with root lesions and advancing to individual tree mortality or mortality in patches (Kile et al., 1991). While the incidence of *Armillaria* root disease in the western boreal forest has not been well documented (Mallett, 1990), the disease is known to cause growth loss and mortality (Mallett and Volney, 1999). There are three species of *Armillaria* found in the prairie provinces, *A. ostoyae* (Romagn.) Herink, *A. sinapina* Bérubé and Dessurreault, and *A. calvescens* Bérubé and Dessurreault. All have been isolated from diseased trembling aspen (Mallett, 1990, 1992). No attempts were made to identify the *Armillaria* species in this study. Primary disease may not always be visible (Kile et al., 1991) and, in many cases, visible versus actual incidence of *Armillaria* root disease can be completely different. A survey of conifer plantations in Ontario for *Armillaria* root disease found that on average 58% of the trees were infected with the disease but were without aboveground symptoms (Whitney et al., 1989). In British Columbia incidence of *Armillaria* root disease in asymptomatic conifer plots were 6, 24, and 15% in dry, moist, and wet climatic regions, respectively (Morrison et al., 2000).

The other pests encountered in this study such as large aspen tortrix, poplar peniophora, false tinder conk, and hypoxylon canker are considered relatively serious pests in the study area while aspen leaf beetle (*Chrysomela crotchi* Brown), aspen leafroller, American aspen beetle (*Gonioctena americana* [Schaeff.]), and poplar borer are generally considered of minor importance (Ives and Wong, 1988; Hiratsuka, 1987). Outbreaks of large aspen tortrix occur periodically in the region, last less than 3 years, and have caused moderate losses in some parts of the study area (Prentice, 1955; Brandt, 1994, 1995a,b; Cerezke and Volney, 1995). There is no information in the literature associating the incidence of this defoliator with the specific stand conditions we examined. Witter and Waisanen (1978), however, report that early flushing clones of trembling aspen are preferred over late flushing clones by large aspen tortrix. Our results indicate a relationship between hypoxylon canker and stand density, which is consistent with the results of Anderson (1952) and Anderson and Anderson (1968). Other factors related to the incidence of this canker include previous defoliation by forest tent caterpillar, presence of poplar borer, and moisture stress (Bagga and Smalley, 1974; Anderson and Martin, 1981), but there is conflicting information in the literature (Manion and Griffin, 1986). While leafblotch miner is considered minor, large outbreaks of this insect have occurred in the study area as well as in Minnesota and Ontario (Martin, 1956; Auerbach, 1991). Our findings linking leafblotch miner with smaller, younger trees are corroborated by observations made in Ontario (Martin, 1956).

5. Conclusions

Manion (1991) defines three types of factors that influence diseases of complex biotic and abiotic origins.

These factors are designated as predisposing, inciting, and contributing. Predisposing factors are long-term factors that change slowly over time and reduce a tree's ability to defend against injurious agents. Inciting factors are more short-term and produce physiological responses in a tree. Contributing factors are usually secondary or opportunistic organisms that attack a tree weakened by other agents. Age is most likely the principal predisposing factor affecting the health of trembling aspen in the study area. Forest tent caterpillar, drought, and *Armillaria* root disease are inciting factors. While forest tent caterpillar and drought are common in the study area, the evidence we provide here and supported by others indicates that impacts of these factors are more severe in the transitional forest than in the boreal forest. Differences in the incidence and severity of forest tent caterpillar and drought along a gradient from the transitional forest to the true boreal forest may account for the differences in trembling aspen health observed in the region. The inclusion of *Armillaria* root disease as an inciting factor goes against the theory described by Manion but is included here because the pathogen was a significant factor even when controlling for the effects of forest tent caterpillar defoliation. This study supports the hypothesis that *Armillaria* root disease is a virulent pathogen and not just a secondary pest. The other pests encountered in this study are contributing factors. While the mechanism in which these various biotic and abiotic factors interact between periodic episodes of drought and forest tent caterpillar defoliation is unknown, their combined influence ultimately affects the health of trembling aspen in the study area.

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